

Population dynamics of *Bythotrephes cederstroemii* in south-east Lake Michigan 1995–1998

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SUMMARY

1. Population characteristics (density, size, reproductive patterns) of the predatory cladoceran *Bythotrephes cederstroemii* in south-east Lake Michigan were monitored at an offshore station (110 m) in 1995–98 and at a nearshore station (45 m) in 1997–98.
2. The mean density of *B. cederstroemii* at the offshore station was generally highest in July–September ($145\text{--}914\text{ m}^{-2}$) and at the nearshore station in October–November ($168\text{--}1625\text{ m}^{-2}$). In 1995 and 1998, density was also high at the offshore station in November ($211\text{--}284\text{ m}^{-2}$). Fish predation may limit *B. cederstroemii* in nearshore regions in the summer. The maximum annual densities of *B. cederstroemii* for 1995–98 were generally similar to those reported from the late 1980s, when the species arrived in Lake Michigan.
3. Body size increased rapidly each year to a maximum in August. Thereafter, body size declined and converged for stage-2 and 3 individuals, suggesting food scarcity or size-selective fish predation was affecting large individuals.
4. Most reproduction occurred asexually (90%), and by stage 2 or 3 females (99%). Asexual brood size was highest when *B. cederstroemii* first appeared each year, and decreased in August, when larger neonates were produced. There appeared to be differences in reproductive mode for stage 2 and 3 females, with a higher percentage of stage 2 females reproducing sexually.

Keywords: *Bythotrephes cederstroemii*, exotic species, Lake Michigan, parthenogenesis, resting egg

Introduction

Bythotrephes cederstroemii Schoedler, a predaceous cladoceran native to northern Europe and Asia, is characterized by a long caudal spine that makes up to 70% of the total body length (Rivier, 1998). The caudal spine contains one to four pairs of barbs depending on instar (Yurista, 1992; Burkhardt, 1994). *Bythotrephes cederstroemii* reproduces asexually in summer and sexually later in the year, when resting eggs are produced that overwinter and hatch the following

summer or later (Yurista, 1992; Rivier, 1998). Some works suggest that *B. cederstroemii* in the Great Lakes and *B. longimanus* might actually be one species with variable morphology (Berg & Garton, 1994).

Bythotrephes cederstroemii was first found in the Laurentian Great Lakes in 1982 in Lake Ontario (Fricker & Abbott, 1982). It was presumably transported to the U.S.A. through contaminated ship ballast water (Jin & Sprules, 1990). By 1987, *B. cederstroemii* was present in all the Great Lakes (Bur, Klarer & Krieger, 1986; Lange & Cap, 1986; Lehman, 1987; Cullis & Johnson, 1988; Evans, 1988). The arrival of *B. cederstroemii* in Lake Michigan in 1986 has been considered a major factor causing changes to the zooplankton community and its food-web (Lehman, 1991; Burkhardt & Lehman, 1994),

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although the extent of these changes is disputed (Sprules, Riessen & Jin, 1990).

Bythotrephes cederstroemii population dynamics, including density, population structure and reproductive characteristics, were monitored in south-east Lake Michigan during 1995–1998. In order to understand the changing food-web dynamics of Lake Michigan, it is necessary to understand the population dynamics of a species such as *B. cederstroemii* once it has become fully established in the lake. Understanding *B. cederstroemii* population dynamics after it has been in the lake for over a decade may also help predict the implications of invasions by non-native species such as *Cercopagis pengoi* Ostroumov, another spiny-tailed predaceous cladoceran that has already been found in large numbers in the Great Lakes (MacIsaac et al., 1999).

Methods

Bythotrephes cederstroemii were collected from south-eastern Lake Michigan at an offshore site (110 m water depth) during 1995 and 1998 and from a nearshore site (45 m water depth) in 1997 and 1998. The nearshore and offshore stations were located about 10 and 20 km off Muskegon, Michigan, respectively. In 1995 and 1996, sampling was conducted four times annually between June–November 1995 and April–December 1996. In 1997 and 1998, collections were taken at each station monthly, starting when *B. cederstroemii* had appeared in regular zooplankton tows in the early summer, until December.

Replicate samples were collected during the day with a 1-m diameter plankton net (363- μ m mesh) towed vertically from just above the bottom to the surface. *Bythotrephes cederstroemii* were anesthetized with carbonated water and preserved in 10% sugar-buffered formalin. Water temperature was recorded using a Seabird CTD at each station each month and when *B. cederstroemii* were collected. Epilimnial temperature was measured because *B. cederstroemii* are usually found in or above the metalimnion (Lehman, 1987). To determine prey availability, zooplankton were collected with vertical tows from just above the bottom to the surface using a 0.5-m diameter plankton net (153- μ m mesh). A sub-sample of at least 200 organisms was counted for each zooplankton sample. The density of cladocerans was measured because they are the main prey for

B. cederstroemii in Lake Michigan (Vanderploeg, Liebig & Omair, 1993; Lehman & Branstrator, 1995; Schulz & Yurista, 1999).

Having counted all *B. cederstroemii*, areal density was calculated to allow comparison between depths and with previous data collected from south-eastern Lake Michigan (Lehman, 1991; Lehman & Caceres, 1993). Body and spine length, not corrected for shrinkage, were measured and the number of spine barbs counted for up to 100 individuals per sample (Burkhardt, 1994). The number of barbs on the tail spine increases with instar (Burkhardt, 1994). The size of sexual and asexual broods was determined for reproductive females. Resting eggs result from sexual reproduction and are distinguished from asexual embryos by their thick, hard, yellowish shells (Yurista, 1992). Developmental stages of embryos produced asexually were not differentiated (Yurista, 1992). Stage-1 animals (neonates) were categorized as originating from sexual or asexual reproduction based on tail spine morphology. *Bythotrephes cederstroemii* originating from sexual reproduction have straight spines, whereas those produced asexually have a distinctive kink in the spine (Yurista, 1992).

Body and spine lengths for each developmental stage from each year were compared across sampling dates and sites using analysis of variance (ANOVA) (SYSTAT 8.0). Mean brood size for females reproducing sexually or asexually each year was compared across sampling dates and sites using ANOVA. The proportion of females reproducing sexually and asexually was compared between sites and among years using categorical analysis. The *P*-values of 0.05 were considered significant for all tests.

Results

Temperature and zooplankton abundance

The epilimnion formed each year in May or June and water temperature peaked during July or August (Fig. 1). Maximum epilimnial temperature was higher in 1995 (25 °C) and 1998 (22 °C) than in 1996 (20 °C) and 1997 (18 °C). By late October each year, the metalimnion had begun to deepen and the epilimnion extended to depths of 28–40 m.

Daphnia spp. (mostly *D. galeata mendotae* Birge) and Bosminidae (mostly *B. longirostris* O.F. Moeller)

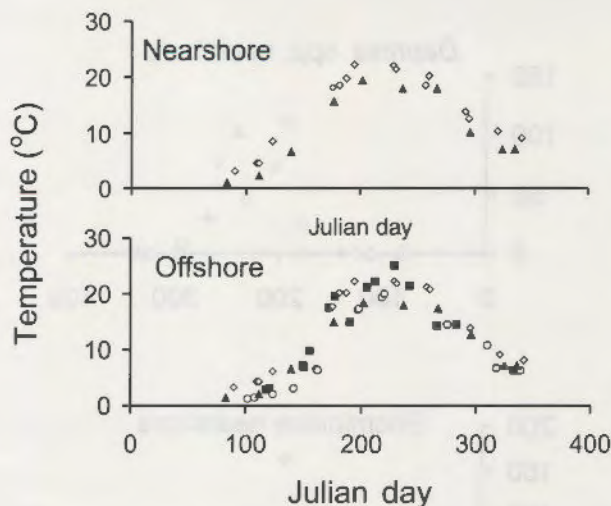


Fig. 1 Mean epilimnetic water temperature for an offshore (1995–98) and a nearshore (1997–98) site in south-eastern Lake Michigan. ■, 1995; ○, 1996; ▲, 1997; ◇, 1998.

abundance began to increase in June or July each year (Fig. 2). The density of *Daphnia* spp. was highest during August or September at the offshore site, and in July or August at the nearshore site. The density of Bosminidae was highest in July or August at both sites. At the nearshore site, cladoceran density recovered somewhat in the autumn following a decline after the summer peak. The densities of *Daphnia* spp. and Bosminidae were higher nearshore in July but were higher offshore in August and September, except in 1997 when Bosminidae were rare at the offshore site throughout the year.

Density

Bythotrephes cederstroemii was not found in zooplankton samples until water temperature reached 17–20 °C. At the offshore site, the mean density of *B. cederstroemii* rose rapidly to a maximum between early July and September, depending on the year (Table 1). In 1997, a high density of *B. cederstroemii* was sustained into October. In November 1995 and 1998, *B. cederstroemii* densities rose following a decline after the summer peak. The mean density of *B. cederstroemii* at the nearshore site reached a maximum in October 1997 and November 1998. At the nearshore site, density was generally lower than offshore, except in November 1998 when the highest density of the study occurred.

Population structure

The population structure of *B. cederstroemii* differed seasonally (Table 1). In general, neonates (stage-1) comprised at least a third of the *B. cederstroemii* caught during the first 1 or 2 months after they appeared in samples. Only four individual stage-4 *B. cederstroemii* were found in 1995–98. In 1997, stage-2 animals were overwhelmingly dominant from September to December at both sites.

Overall, 75% of stage-1 *B. cederstroemii* originated from asexual reproduction (Table 1). The predominance of asexually produced individuals early in the year suggests that small numbers of *B. cederstroemii* must have been present in the water column before they appeared in our samples. Sexually produced individuals caught in July and August probably originated from resting eggs produced the previous year or earlier, because females with resting eggs were generally not found until August each year. The body length of stage-1 individuals did not differ between asexually and sexually produced animals, but asexually produced stage-1 animals had significantly longer tail spines.

Mean body length for each stage differed significantly among sampling dates each year except for stage-1 in 1997 (nearshore) and stage-3 in 1996 (Fig. 3). Mean spine length also differed significantly among sampling dates each year except for stage-1 in 1997 (nearshore) and 1998 (offshore), and stage-3 in 1996 and 1997 (nearshore and offshore) (Fig. 3). Body length was generally lowest during the initial appearance of *B. cederstroemii*, and increased rapidly to a maximum in August each year. In 1998 and 1996, body length was also relatively high in November or December, respectively. Trends in spine length among dates were variable and different from those in body length. Although body length differed significantly among developmental stages each year, the difference between stage-2 and 3 individuals was less apparent than between stage-1 and 2 individuals, particularly in the late summer and autumn. No apparent convergence in spine lengths was noted for stage-2 and 3 individuals.

Mean body length for stage-1 and 3 individuals differed significantly between the nearshore and offshore sites in both 1997 and 1998. Mean spine length for stage-1 individuals differed significantly between the near- and offshore sites in 1998. No other

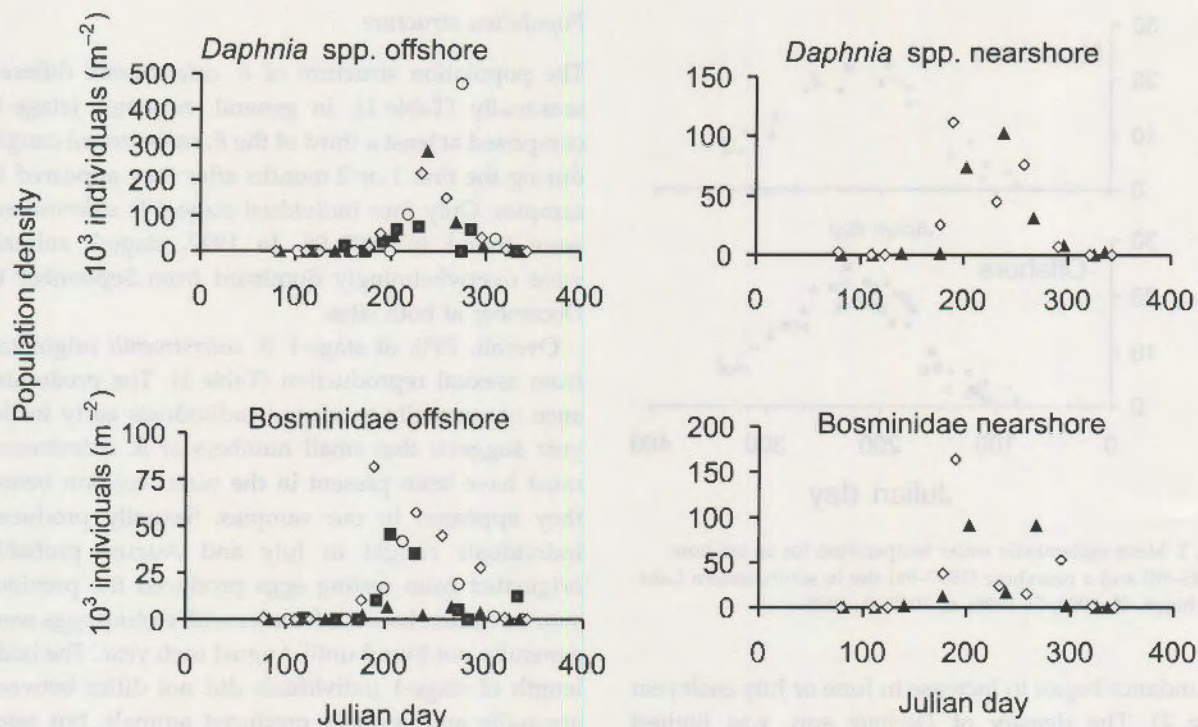


Fig. 2 Mean density of *Daphnia* spp. and *Bosminidae* at an offshore (1995–98) a nearshore (1997–98) site in south-eastern Lake Michigan. ■, 1995; ○, 1996; ▲, 1997; ◇, 1998.

differences in body or spine length for individuals from the nearshore and offshore sites were found. In all instances where there were differences, the body and spine lengths were greater at the offshore site.

Reproduction patterns

The majority (90%) of the females with broods were reproducing asexually. About 45 and 54% of the females with asexual broods were stage-2 and 3 individuals, respectively. In contrast, about 67 and 33% of the females with sexual broods were stage-2 and 3 individuals, respectively. During June and July, when *B. cederstroemii* first appeared, nearly all reproduction was asexual (99%) (Fig. 4). By July or August, except in 1996, a small percentage of females (6–14%) was carrying resting eggs (Fig. 4). The proportion of females that reproduced sexually peaked in November and December at 12–31% (Fig. 4).

Asexual brood sizes differed significantly among dates sampled each year. Asexual brood size was at an annual maximum in June or July, before declining in August (Fig. 5). Asexual brood size did recover somewhat in October 1998. Sexual brood size only

differed significantly among dates sampled at the offshore site in 1997, when it was highest in September (Fig. 5). Based on the number of eggs per reproductive female, mean sexual brood size was 5.9 resting eggs/female and was significantly larger than mean asexual brood size (3.9 embryos/female). Asexual broods were significantly larger in stage-3 females (4.2) than in stage-2 (3.5); sexual broods were significantly larger in stage-2 females (6.1) than in stage-3 (5.4). Neither asexual nor sexual brood sizes differed significantly between the nearshore and offshore sites in 1997 or 1998. About 90% of reproduction was asexual at both the nearshore and offshore sites.

Discussion

Bythotrephes cederstroemii were first observed each year in late June or July when water temperature had reached 17–20 °C. *Bythotrephes cederstroemii* numbers offshore increased rapidly to a maximum between July and September. The density of *B. cederstroemii* was generally lower nearshore than offshore, and nearshore density did not peak until October or November. The presence of asexually produced neonates during

Table 1 Mean density of *Bythotrephes cederstroemii* \pm 1 SE (replicate tows), population structure (percent by developmental stage), and percentage of stage-1 individuals that developed from asexual and sexual reproduction from an offshore (1995–98) and nearshore (1997–98) site in south-eastern Lake Michigan

Depth	Year	Day	Density (no m ⁻²)	Stage 1 (%)	Stage 2 (%)	Stage 3 (%)	Stage 4 (%)	Stage-1 (%)	
								Asexual	Sexual
Offshore	1995	18 June	5 (1)	0	38	38	25	0	0
		31 July	145 (56)	36	28	36	0	89	11
		17 August	57 (4)	19	27	54	0	94	6
		13 November	228 (73)	38	48	14	0	82	18
	1996	11 April	0	0	0	0	0	0	0
		17 July	22	71	12	18	0	100	0
		5 August	406 (93)	47	24	29	0	89	11
		4 December	20 (4)	22	59	19	0	43	57
	1997	21 July	33 (6)	44	19	36	0	74	26
		26 August	317 (13)	36	42	23	0	62	38
		24 September	914 (155)	18	64	18	0	66	34
		23 October	687 (156)	24	56	20	0	80	20
		21 November	87 (26)	19	73	8	0	31	69
		2 December	44 (17)	13	70	17	0	22	78
	1998	26 June	4 (1)	28	28	28	14	50	50
		7 July	212 (7)	38	35	27	0	71	29
		19 August	164 (15)	8	56	36	0	88	12
		14 September	56	21	40	40	0	75	25
		22 October	40 (8)	38	28	33	0	100	0
		17 November	284 (212)	5	36	59	0	50	50
		8 December	31 (4)	22	28	49	0	64	36
Nearshore	1997	21 July	0	0	0	0	0	0	0
		26 August	96 (57)	10	48	42	0	81	19
		24 September	36 (2)	48	24	29	0	75	25
		23 October	168 (70)	7	74	19	0	93	7
		21 November	11 (1)	36	41	23	0	62	38
		2 December	48 (43)	10	81	8	0	40	60
	1998	26 June	25 (5)	32	18	50	0	92	8
		7 July	71 (32)	52	20	28	1	71	29
		19 August	119 (11)	6	69	25	0	75	25
		14 September	4 (1)	14	28	57	0	100	0
		22 October	13 (6)	20	35	45	0	75	25
		17 November	1625 (52)	4	41	55	0	67	33
		8 December	15 (2)	22	61	17	0	40	60

June and July indicates that *B. cederstroemii* from resting eggs had appeared somewhat earlier in the year. However, density was probably below detection limits for the sample size used (Ketelaars *et al.*, 1995).

Fish predation may have been an important factor limiting *B. cederstroemii* abundance at the nearshore site. Fish predation has been implicated in limiting large cladocerans in nearshore areas of Lake Michigan in the summer (Evans, Hawkins & Sell, 1980; Evans, 1990) and *Bythotrephes* spp. are known to be vulnerable to fish in their native Europe (Rivier, 1998) and in the Great Lakes (Mills *et al.*, 1992). Fish density in

Lake Michigan in the summer is higher nearshore than offshore (Brandt *et al.*, 1991), and predation demands by alewife *Alosa pseudoharengus* Wilson, the main fish predator on *B. cederstroemii* in Lake Michigan, are highest in the summer and early autumn (Stewart & Binkowski, 1986; Hewett & Stewart, 1989; Rand *et al.*, 1995). In addition to direct predation on *B. cederstroemii*, alewife likely competed with *B. cederstroemii* for cladoceran prey in the summer (Makarewicz *et al.*, 1995). A release from fish predation and competition in the late autumn may explain the late season increase of *B. cederstroemii* at the nearshore

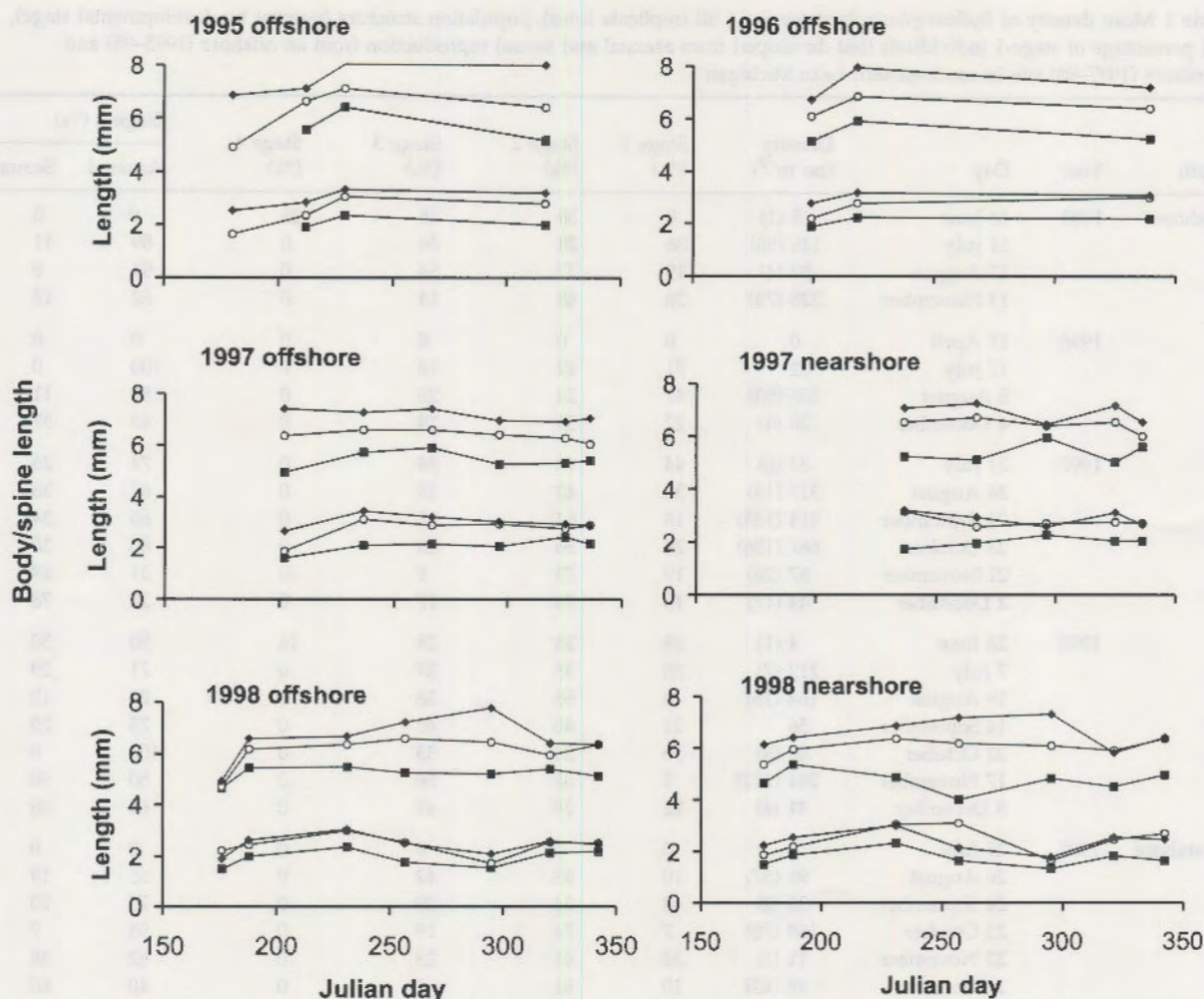


Fig. 3 *Bythotrephes cederstroemii* body (lower lines) and spine (upper lines) lengths at an offshore (1995–98) and a nearshore (1997–98) site in south-eastern Lake Michigan. ■, stage-1; ○, stage-2; ♦, stage-3.

site (Makarewicz & Jones, 1990). Alewife abundance in Lake Michigan declined in the early 1980s (McDonald, Crowder & Brandt, 1990; Fabrizio, Raz & Bandekar, 2000), so any future recovery in alewife numbers that occurs following recent decreases in salmonid stocking may affect *B. cederstroemii* abundance in nearshore areas (Makarewicz & Jones, 1990).

Bythotrephes cederstroemii abundance in south-east Lake Michigan was variable from year-to-year in 1995–1998, but there was no overall trend and no strong difference from their density soon after colonization of the lake in the 1980s. *Bythotrephes cederstroemii* were first found offshore (100 m) in south-eastern Lake Michigan near Grand Haven, Michigan in August 1986 at a density of 76 m^{-2} and rapidly increased to 290 m^{-2} by September 1986 (Lehman,

1987). Annual maximum abundance of *B. cederstroemii* offshore of Grand Haven during the summer (July–September) between 1987 and 1989 ranged from 239 to 681 m^{-2} (Lehman, 1991; Lehman & Caceres, 1993). In 1995–1998, the maximum density of *B. cederstroemii* during July–September ranged from 145 to 914 m^{-2} offshore of Muskegon. Muskegon is located about 20 km north of Grand Haven. Density at nearshore sites off Grand Haven (20–45 m) in the summer peaked at 61 m^{-2} in 1986 and 46 m^{-2} in 1987 (Lehman, 1987, 1991), compared with 96 m^{-2} in 1997 and 119 m^{-2} in 1998. The density of *B. cederstroemii* was also relatively high in November 1995–98, ranging from 87 to 284 m^{-2} offshore, and 11 to 1625 m^{-2} nearshore. *Bythotrephes cederstroemii* had previously been assumed to disappear after October (Sprules

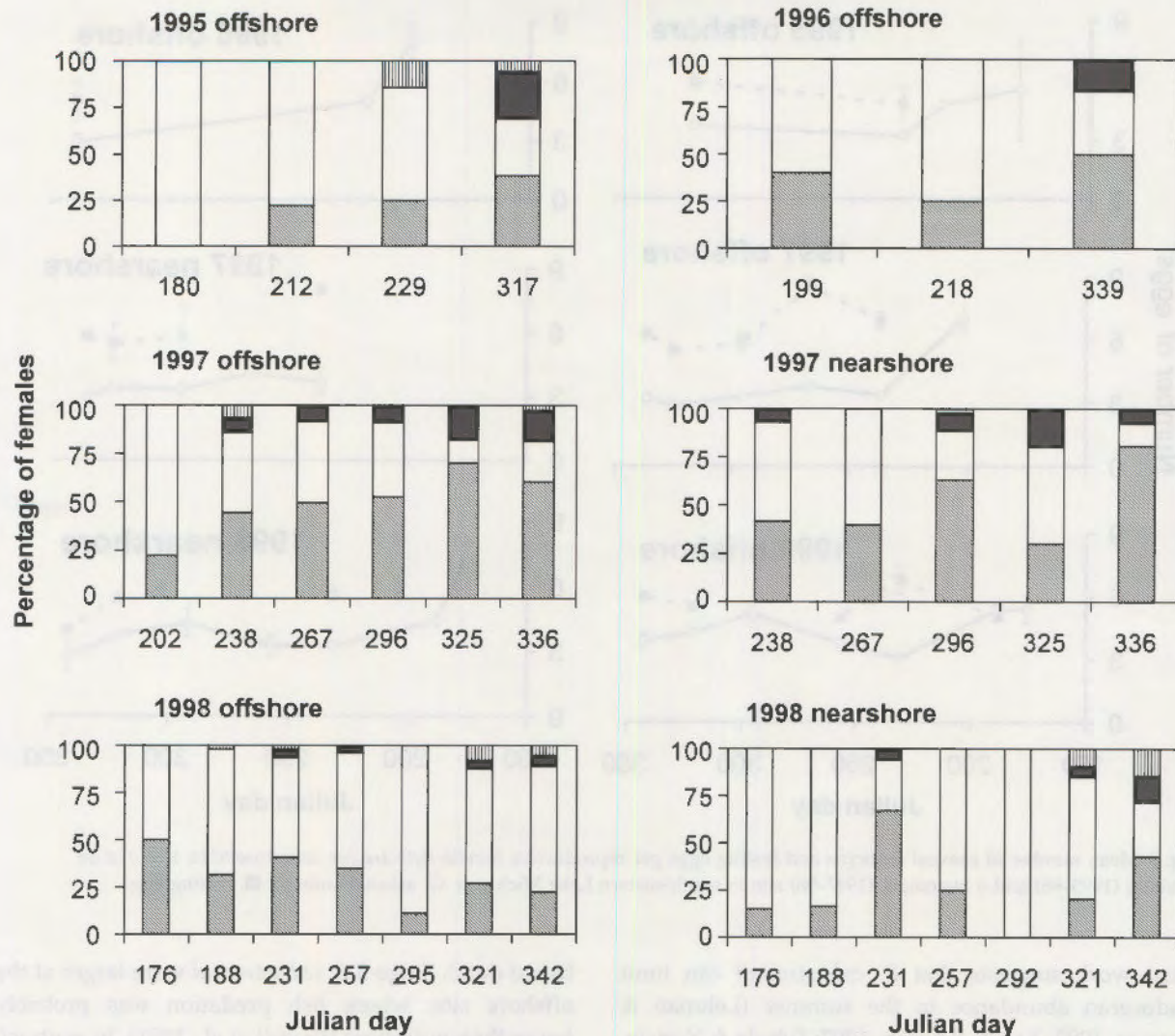


Fig. 4 Percentage of stage-2 and 3 female *Bythotrephes cederstroemii* that reproduced asexually and sexually at an offshore (1995–98) and a nearshore (1997–98) site in south-eastern Lake Michigan. ▨, stage-2 asexual; □, stage-3 asexual; ■, stage-2 sexual; ▩, stage-3 sexual.

et al., 1990; Rivier, 1998) and little sampling has been performed after September in most studies.

The mean body length of *B. cederstroemii* generally increased rapidly from June or July to a maximum in August and a subsequent decline. The increase in body length in mid-summer has been attributed to direct and indirect relationships with water temperature (Burkhardt, 1994; Ketelaars *et al.*, 1995). Maximum body length occurred when water temperature was at its annual maximum of 18–25 °C. Maximum rate of food consumption by *B. cederstroemii* occurs at 15–20 °C (Burkhardt, 1994) and could be the reason for the increased growth observed in the summer. The

abundance of *Daphnia* and *Bosminidae*, the presumed preferred prey of *B. cederstroemii*, were also increasing as water temperatures increased in July and August, so an increase in food availability could also explain increased body size of *B. cederstroemii* (Burkhardt, 1994).

After August, body length decreased and mean body size of stage-2 and 3 individuals converged. Similar results were attributed to prey scarcity in an inland Canadian lake (Yan & Pawson, 1998). In contrast, where food was not limited in a European lake, body size of stage-2 *B. longimanus* continued to increase throughout the year (Straile & Halbach, 2000).

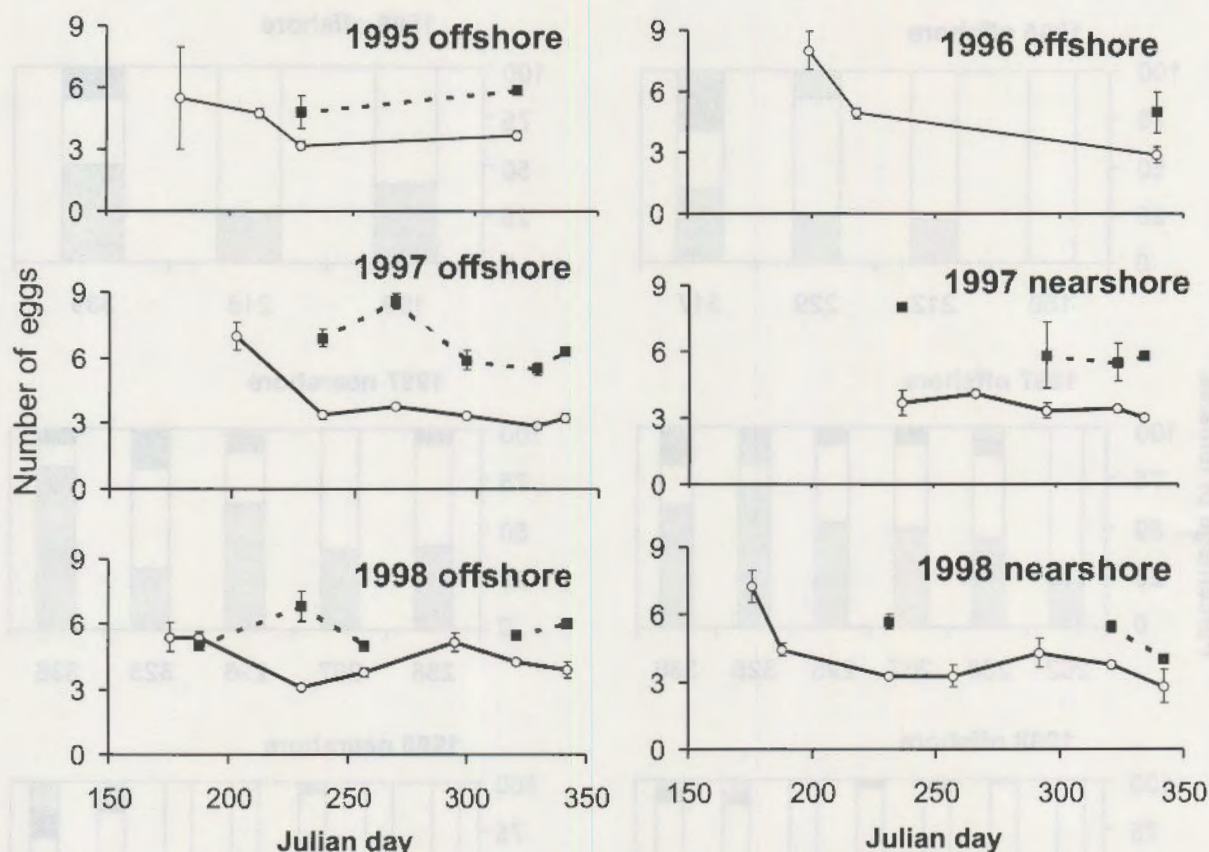


Fig. 5 Mean number of asexual embryos and resting eggs per reproductive female *Bythotrephes cederstroemii* (± 1 SE.) at an offshore (1995–98) and a nearshore (1997–98) site in south-eastern Lake Michigan. \circ , asexual embryo; \blacksquare , resting egg.

Most work suggests that *B. cederstroemii* can limit cladoceran abundance in the summer (Lehman & Caceres, 1993; Yan & Pawson, 1997; Schulz & Yurista, 1999). Additionally, in the autumn and early winter, when Cladocera are scarce, *B. cederstroemii* would need to feed on copepods. *Bythotrephes cederstroemii* are probably poor predators of cyclopoid copepods (Vanderploeg *et al.*, 1993), but they are known to consume calanoid copepods and copepod nauplii (Vanderploeg *et al.*, 1993; Schulz & Yurista, 1999). It is also possible that *B. cederstroemii* are cannibalistic when other cladocerans are absent (Rivier, 1998; Schulz & Yurista, 1999).

In addition to prey scarcity, size-selective fish predation also appears to be a factor resulting in the decrease in body size after August and the convergence in body size of stage-2 and 3 individuals. Adults of the alewife are size-selective predators (Wells, 1970) and consume the largest *B. cederstroemii* available (8–12 mm total length) (S. Pothoven, unpub-

lished data). Stage-3 *B. cederstroemii* were larger at the offshore site, where fish predation was probably lower than nearshore (Brandt *et al.*, 1991). In contrast, size-selective fish predation was not considered to be a factor in determining body size of *B. cederstroemii* in the Canadian Harp Lake (Yan & Pawson, 1998).

Seasonal trends in spine length were less clear than in body length. Spine length was greatest in August 1995 and 1996, but the maximum was later in the year in 1997 and 1998. The length of the tail spine of *B. cederstroemii* may vary with predation risk (Barnhisel, 1991). In a Dutch reservoir with few fish, spine length did not differ between developmental stages (Ketelaars *et al.*, 1995). An increase in spine length in later instars may be an effective anti-predator defence against small fish (Barnhisel, 1991), but is probably ineffective against larger predators such as adults of the alewife.

Most females (90%) reproduced asexually and, based on spine morphology of stage-1 individuals,

most (75%) originated from parthenogenesis. Parthenogenesis allows a species to respond rapidly to favourable environmental conditions (Rivier, 1998). Sexual reproduction by *B. cederstroemii* was originally thought to be confined to the autumn (Sprules *et al.*, 1990) but, in 1995–98, females with resting eggs appeared as early as July or August, as was observed in south-east Lake Michigan in 1990–91 (Burkhardt, 1994). The proportion of females reproducing sexually peaked in late autumn, probably as a result of changes in photoperiod or temperature (Herzig, 1985).

Asexual brood size was highest when *B. cederstroemii* first appeared in June or July and then decreased by August. The decrease in brood size occurred when body size was highest and was accompanied by a corresponding increase in the size of neonates. Similar results were observed for *B. longimanus* in Europe (Ketelaars *et al.*, 1995; Straile & Halbach, 2000). The change may be a response to gape-limited predation (Straile & Halbach, 2000). Although gape-limited juvenile fish can be numerous in Lake Michigan in summer, larger size at reproduction and larger neonates would make both reproductive females and neonates more vulnerable to non-gape-limited adult alewife (Mills *et al.*, 1992; Straile & Halbach, 2000). The decrease in brood size and increase in neonate size may also be attributable to food scarcity, because larger neonates may be more resistant to starvation (Ketelaars *et al.*, 1995). Although *Daphnia* and Bosminidae were relatively abundant in August, there may still have been intense predation pressure on these prey (Burkhardt & Lehman, 1994; Makarewicz *et al.*, 1995). The appearance of females with resting eggs in July and August suggests that food limitation could favour the production of fewer, larger asexual neonates (Burkhardt & Lehman, 1994; Yan & Pawson, 1998).

In contrast with earlier work on Lake Michigan, we noted a high percentage of stage-2 females that were reproductive (Yurista, 1992; Lehman & Branstrator, 1995). Although reproduction by stage-2 females can indicate good environmental conditions (Ketelaars *et al.*, 1995), this is not necessarily true (Yan & Pawson, 1998). Alternatively, reproduction by stage-2 females in Lake Michigan has also been considered an anomaly related to missing barb formation during a moult (Yurista, 1992), but this has been discounted in other studies (Yan & Pawson, 1998).

There appeared to be differences in the mode of reproduction in stage-2 and 3 females. The proportion

of females that reproduced sexually, and the size of broods of resting eggs, were higher in stage-2 individuals than in stage-3. In contrast, asexual brood size was higher in stage-3 females than in stage-2. Food limitation or size-selective fish predation may favour individuals that produce resting eggs earlier in life. Resting eggs remain dormant during adverse conditions and can pass through a fish if the female is eaten (Herzig, 1985; Yurista, 1997). Broods of resting eggs were also larger on average than asexual broods. In contrast, continued asexual reproduction by larger individuals may produce more rapid population growth if the environment remains favourable.

The density of *B. cederstroemii* in south-eastern Lake Michigan has not changed dramatically since 1986, when they were first found in the lake. Factors such as fish predation pressure and prey scarcity in the summer may limit the annual production of *B. cederstroemii* and affect its life history, however. The recent invasion of Lake Michigan by another predatory cladoceran, *Cercopagis pengoi* Ostroumov, will probably affect *B. cederstroemii* and other zooplankton by placing additional predation pressure on offshore zooplankton populations (MacIsaac *et al.*, 1998).

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